

Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* (Araneae: Ctenidae) in a Central Amazonian rainforest

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Abstract. *Phoneutria* is one of the most medically important spider genera; however, its ecology is poorly known. In Amazonian upland rainforests, there are two sympatric species of the genus *Phoneutria*, *P. reidyi* (F.O. Pickard-Cambridge 1897) and *P. fera* Perty 1833. For 15 months we collected data on the spatial distribution, use of habitat (activity on the ground or vegetation) and temporal changes in body size structure in a forest reserve near Manaus city in three distinct habitats: dense forest, located on the plateaus on yellow latosol; swamp forest, located in the valleys; and heath forest or "campinarana," on dry white sand soil in the Reserva Florestal Ducke. A total of 239 *P. reidyi* and 239 *P. fera* were captured in nocturnal searches during their period of activity. There were significant differences between the two species: 1) *P. reidyi* existed in higher abundance in the swamp forest than in the dense forest areas and was almost absent in the heath forest, while *P. fera* existed in similar abundance in the three habitats. 2) During their development, members of both species used the vegetation as an area of activity, but the subadults and adults of *P. reidyi* were less often found on the ground than the subadults and adults of *P. fera*. 3) *P. reidyi* more frequently used small or acaulescent palms as a substrate, and its abundance was directly related to the abundance of these palms, independent of the habitat, while *P. fera* did not show such relationship. 4) There was a strong temporal variation in the body size structure of the *P. reidyi* population indicating seasonal reproduction, but there was no evidence of seasonal reproduction by *P. fera*. We suggest that the differences in the use of habitat and in the seasonality of reproduction are related to the avoidance of intraguild predation between these species.

Keywords: Amazon, "banana-spider," coexistence, life cycle, microhabitat preferences, wandering spiders

Spiders of the genus *Phoneutria* are large nocturnal hunting species common in South American forests and in synanthropic areas close to these forests (Lucas 1988; Folly-Ramos et al. 1998). They are considered aggressive and among the medically most important spiders in the world, on the basis of the number of serious human accidents (Maretic 1987; Lucas 1988, 2002; Vetter & Isbister 2008). Despite their medical importance, little is known about their ecology, although they are frequently abundant in forests where they occur.

Bücherl (1969, 1980), Bücherl et al. (1969), Lucas (1969, 1988), Folly-Ramos et al. (1998), and Almeida et al. (2000) presented data on development, activity, seasonality of reproduction, and habitat use of *Phoneutria nigriventer* (Keyserling 1891). In southeastern Brazil, Bücherl (1969) and Lucas (1988) found that *Phoneutria keyserlingi* (F.O. Pickard-Cambridge 1897) and *P. nigriventer* reach maturity in three years, with a marked seasonal reproduction. These studies were based mainly on synanthropic populations and on animals kept in captivity. Until recently, nothing has been published on the ecology of the Amazonian species *Phoneutria fera* Perty 1833 and *Phoneutria reidyi* (F.O. Pickard-Cambridge 1897), although they have a large distribution in most "terra-firme" forests (Simó & Brescovit 2001). The present paper is part of the first intensive ecological research on the genus in undisturbed areas. In previous publications, we presented results on temporal variation in adult size and sexual dimorphism and notes on natural history (Gasnier et al. 2002; Gasnier et al. 2009).

Phoneutria reidyi and *P. fera* are among the most abundant large spider species in Amazonia. Healthy adults possibly have

few enemies, but the juveniles are probably under constant risk. Most potential predators, such as army ants, spiders of the genus *Ctenus* and frogs, are more abundant on the ground (Vieira & Höfer 1994; Gasnier & Höfer 2001; Menin et al. 2008); therefore, the vegetation may be an important substrate, particularly for juveniles, to avoid predation. Both *Phoneutria* species are frequently found on plants with large leaves, especially acaulescent palms that may attract the spiders because their leaves can sustain their weight and transmit vibrations efficiently (Barth et al. 1988), or because of a higher availability of prey associated with the litter at its base (Vasconcelos 1990).

Differences in the use of habitat, phenology, and general behavior (including prey capture and reproductive behavior) are factors that contribute to the coexistence of spiders (Enders 1976; Uetz 1977; Turner & Polish 1979; Uetz 1991; Cutler & Jennings 1992; Polis & Holt 1992; Wise 1993; Morse 1997; Wise & Chen 1999; Denno et al. 2004; Rypstra & Samu 2005). Areas with the sympatric occurrence of two or more species are not common in the genus (Martins & Bertani 2007); only *P. reidyi* and *P. fera* have a large area of coexistence, apparently most of the Amazonian Region (Simó & Brescovit 2001). Our purpose was to study certain aspects of the ecology of *P. reidyi* and *P. fera* in a forest area, including factors that affect their abundance, use of habitat and life history, and to furnish the basis for understanding their coexistence.

METHODS

Study site and species.—The study was conducted in the Reserva Florestal Ducke, a 10,000 ha primary rainforest

reserve of the Instituto Nacional de Pesquisas da Amazônia (INPA). The fauna and flora of this reserve is one of the most heavily studied in Amazonia (Ribeiro et al. 1999; Adis 2002), including the spider fauna (Höfer & Brescovit 2001). We worked in the northern part of the reserve in the basins of the Barro Branco and Acará streams (2°55'00"–2°56'45"S, 59°57'08"–59°58'41"W). Well-drained clay soils in plateaus and slopes predominate in the basin of Barro Branco stream, with a dense forest (descriptions of vegetation in Guillaumet 1987), and well drained white sandy soils predominate in the basin of Acará stream, with a heath forest or "campinarana" offering a more open canopy than the dense forest. In both areas the soil is sandy and hydromorphic close to the streams, with vegetation called swamp forest or "baixio." In all areas the understory vegetation is relatively open. A description of the study area is presented in Gasnier & Höfer (2001). The average annual temperature is 25.6°C, and the average annual rainfall is 2480 mm. The rainy season occurs between December and May, with the rainiest months in March and April and the driest months from July to September (Marques-Filho et al. 1981). We made our observations and collections between June 1998 and August 1999.

We captured the spiders and observed them at night, with the help of headlamps strong enough to allow for observing spiders' eye reflection (including small individuals) up to a distance of approximately 15–20 m. The body of the spider is visible up to about 3–8 m, depending of the spider's size. The spiders could be located at a considerable height (up to 5 m), but were only captured at heights lower than 3 m. To avoid the effect of rain on the abundance estimates, we did not include data from nights with rain and nights after days with rain. We captured the spiders with glass or plastic vials proportional in size to the spiders (22–80 mm in diameter, 60–140 mm in height, and 20–60 mm opening) and preserved the specimens in 70% ethanol. The material is deposited in the Entomological Collection of INPA.

We initially identified the species in the laboratory based on the reproductive structures of adults (palps and epigyne). However, we realized that the ventral and dorsal color patterns of the body and stripes of the palps allowed us to discriminate among species in the field, including very small juveniles. The patterns are described and illustrated in Martins & Bertani (2007).

Censuses.—We used two types of census: one extensive census to evaluate variation in abundance of spiders in a large area including different habitats, and the other to compare abundance between dense forest on plateaus and swamp forest in valley areas. The extensive census consisted of 60 plots of about 50 × 10 m, separated by a distance of 100 m between plots in a trail of about 9 km inside an area of about 2 × 5 km. We collected spiders four times in each plot in June and October 1998, and in April and August 1999. One person searched for spiders from 0 to 3 m height for approximately 30 minutes in each plot. To investigate the influence of environmental factors on the abundance of the spiders, we counted the number of small or acaulescent palms (> 1 m diameter), collected samples of soil in each plot and calculated the volume of leaf litter. We measured the volume of leaf litter on the ground in the middle of the plot, placing the leaves from a 1-m² area in a graduated container. The volume from

each plot was the mean of the measures made on two occasions.

Since the plots of the extensive census included few places with hydromorphic soils, we performed additional censuses comparing the dense forest areas on plateaus with the swamp forest areas on hydromorphic soils close to streams. We called these surveys plateau-swamp censuses. In these censuses, we searched for spiders in 15 plots on the plateau and in 15 plots in the swamp forest. The effort was standardized as a 2-h search in each plot by one person. The plateau-swamp censuses were made on four occasions, in August and November 1998 and in January and April 1999, but we collected spiders only once in each plot.

Spiders collected apart from the censuses (on other occasions or by someone following behind the person searching) were not considered in the comparisons of abundance among habitats, but were included in the analysis of vertical distribution and population structure. For each spider collected, we recorded the species, size (prosoma length), sex (if adult), and the type and height of the substrate. On the first excursion, small juveniles were not collected because we could not identify small *Phoneutria*.

Statistical Analyses.—The analysis of abundance in a sequence of plots helps to evaluate variation at different scales when the sample unit is not discrete and natural (Ludwig & Reynolds 1988), and to propose hypotheses on factors that affect the abundance. The number of spiders in each plot was low (up to 5); therefore, we used non-parametric tests (Mann-Whitney *U*-test and Spearman rank correlation, r_s). The linear regression between the number of spiders and the number of palms was modeled with Reduced Major Axis because the values of the independent variable were random (Sokal & Rohlf 1995). The interspecific correlation of *P. reidy* and *P. fera* was tested with Spearman rank correlation, and the interspecific association was tested with Yates corrected χ^2 test in a 2 × 2 contingency table with the presence/absence of both species (Ludwig & Reynolds 1988). We used the equality of proportions test to verify whether proportions of spiders on the ground or vegetation differed between species. The seasonality of reproduction was evaluated with a Kolmogorov-Smirnov test, comparing the distribution of body sizes graphically and testing the difference in sizes of juveniles in October 1998 and April 1999, because these were months with large data sets and were six months apart. The statistical package used was SYSTAT 12[®] (Wilkinson 1990).

RESULTS

Abundance Patterns.—A total of 239 *P. reidy*, (181 juveniles, 36 adult males, and 22 adult females) and 239 *P. fera* (respectively 181, 27 and 31) was recorded. However, the proportions of species were different between the two types of censuses. In the 60 plots on the trail of the extensive census, made in areas where well-drained soils predominated, 56 spiders were *P. reidy* and 108 were *P. fera*. In the plateau-swamp census, made in 15 areas of well-drained soil and 15 areas of swamp forest, 136 spiders were *P. reidy* and 55 were *P. fera*. The spiders collected outside the censuses were 47 *P. reidy* and 76 *P. fera*.

In the extensive census, the patterns of abundance were similar within each species, and different between species in

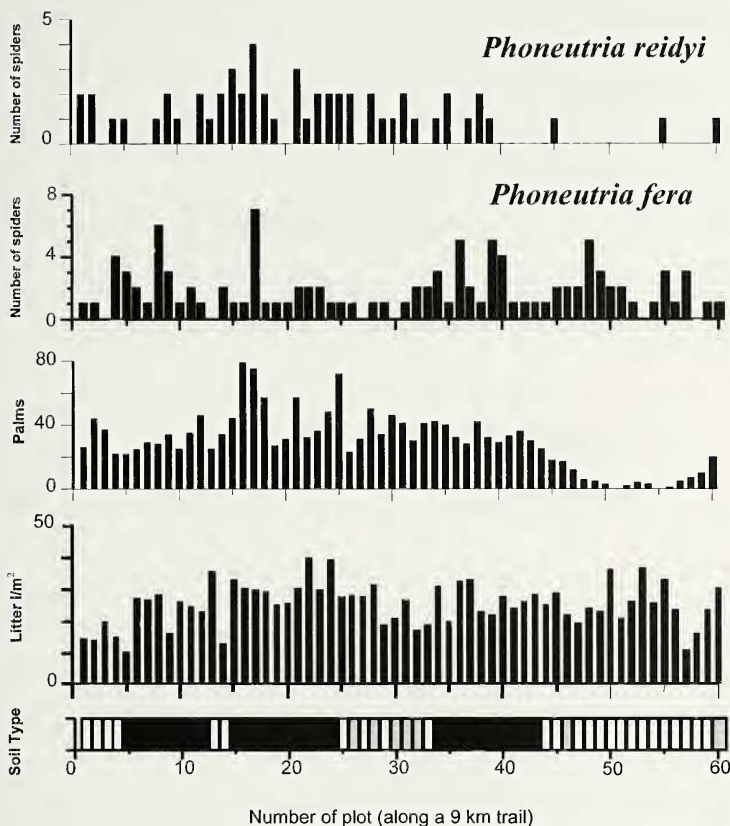


Figure 1.—Superposition of graphs of abundance, showing both species and characteristics of the habitat (number of palms, volume of leaf litter, and type of soil) along the line of extensive census. Each bar corresponds to a transect of 50 m. The soils were categorized as sandy (white), hydromorphic (gray) and clayey (black), and they are closely related to the vegetation types (see Methods).

the four counts throughout one year. *P. reidy*'s pattern was marked by a high abundance (1.36 spiders/100 m) in positions 1–39 and low abundance (0.14/100 m) in the basin of Acará stream (positions 40–60 in Fig. 1), in an area where heath forest over sandy soils predominated. This zone had lower abundances of small or acaulescent palms, but similar amounts of leaf litter compared to the other areas. Compared to *P. reidy*, *P. fera* had a relatively homogeneous abundance along the sequence of plots (1.8/100 m).

In addition, we compared the abundances of spiders between the habitats "dense forest" and "swamp forest", using the plateau-swamp census samples. *P. reidy* was more abundant in the swamp forest (Mann-Whitney *U*-test, $U = 117$, $P = 0.036$), where palms predominate. The abundance of *P. fera* did not differ significantly between these two habitats (Mann-Whitney *U*-test, $U = 67$, $P = 0.051$), with a tendency for smaller numbers in the swamp forest. This difference

suggested that the abundance of small or acaulescent palms was an important factor.

To test the correlation between abundance of palms and abundance of spiders, we used data from the extensive census samples. There was a positive correlation between the number of *P. reidy* and the number of palms (Spearman rank correlation, $r_s = 0.63$, $n = 60$, $P < 0.001$; Fig. 2). As shown above, this relationship is in part a result of differences between habitats for the abundance of palms and the abundance of *P. reidy*, which is weak evidence of a causal relationship. Therefore, we performed two additional tests for the relationship between the number of *P. reidy* and the number of palms, separated by habitat, only in areas with dense forest (Spearman rank correlation, $r_s = 0.67$, $n = 28$, $P < 0.001$) and only in areas with heath forest vegetation (Spearman rank correlation, $r_s = 0.50$, $n = 25$, $P = 0.003$) (sample size in swamp forest was low for this test). These tests show that this positive correlation is

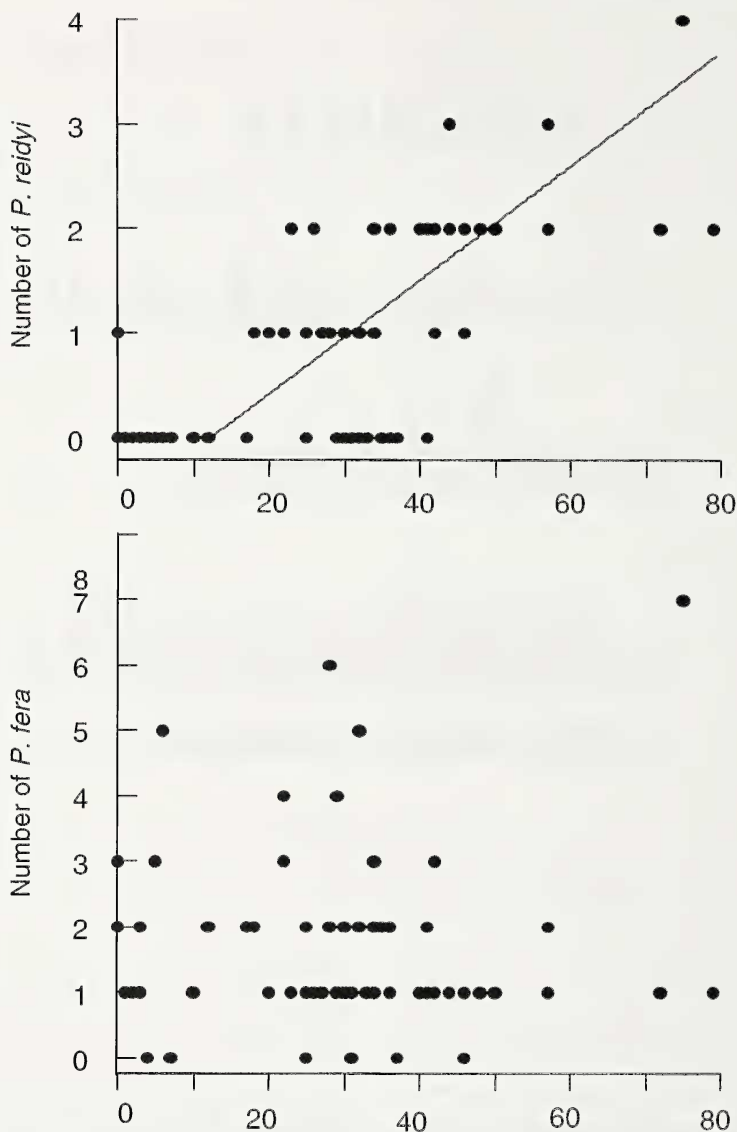


Figure 2.—Relationship between the abundance of palms and the number of spiders in each sample unit. The relationship was significant only for *P. reidy*, for which a regression line is shown (Reduced Major Axis Regression, $Y = -0.671 + 0.0545X$).

independent of the type of habitat for *P. reidy*. The number of *P. fera* and the number of palms did not differ significantly in the extensive census plots (Spearman rank correlation, $r_s = -0.14$, $n = 60$, $P = 0.28$).

We tested the correlation between leaf litter volume and the number of spiders using the extensive census data because the abundance of prey and availability of refuges for spiders may be affected by the volume of leaf litter. We found no

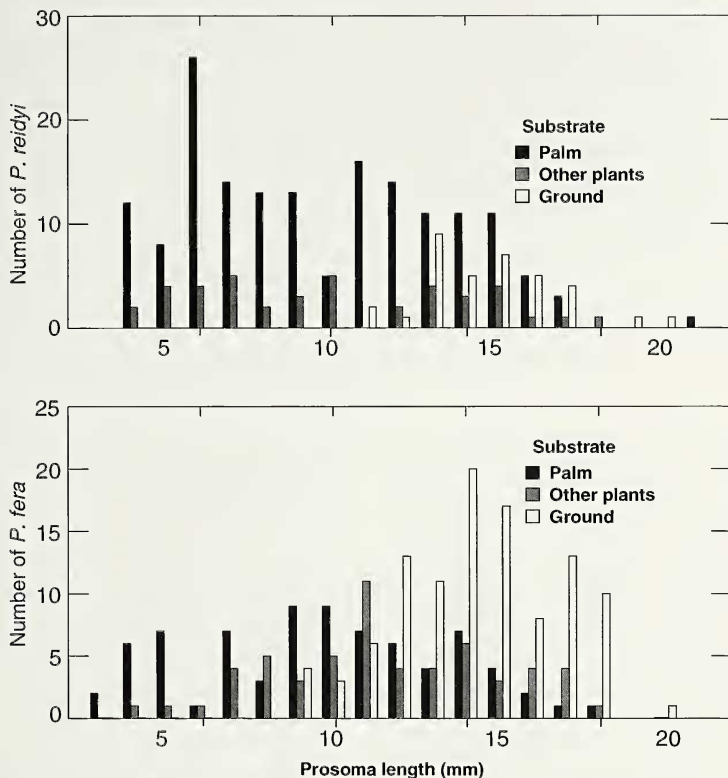


Figure 3.—Frequency of size (prosoma length) categories for *P. reidy* and *P. fera* found on three types of substrate.

significant relationship between the number of spiders and the amount of leaf litter for *P. reidy* (Spearman rank correlation, $r_s = 0.15$, $n = 60$, $P = 0.23$) or *P. fera* (Spearman rank correlation, $r_s = -0.05$, $n = 60$, $P = 0.72$).

To evaluate the interspecific association between these species, we used the sample units of the extensive census ($n = 60$) and of the plateau-swamp census ($n = 30$). There was no significant correlation between the abundance of *P. reidy* and *P. fera* (Spearman rank correlation, $r_s = -0.04$, $n = 90$, $P = 0.72$), nor in the presence/absence (P/A) of the species (PP = 51, PA = 24, AP = 11, AA = 4; $\chi^2 = 0.01$, $P = 0.91$).

Use of the habitat.—Use of habitat changed substantially during the development of both spider species. Juveniles with prosoma length < 9 mm were only found on the vegetation, and spiders gradually increased their use of the ground until they reached adult size (Fig. 3). However, there were differences between species. Use of the vegetation was still preponderant for *P. reidy* with PL > 12mm, while most *P. fera* of this size were found on the ground. Furthermore, *P. reidy* of all spider sizes used small or acaulescent palms much more frequently than other plants, while medium and large *P.*

fera were found on both palms and other plants in similar frequency. A higher proportion of *P. fera* with PL > 12 mm was found on the ground (Proportions test, 45% of 88 *P. reidy* and 67% of 121 *P. fera*; $Z = 3.10$, $P = 0.002$). This difference was independent of the habitat because it was still significant when we restricted the data to swamp forest (Proportions test, 35% of 23 *P. reidy* and 75% of 12 *P. fera*; $Z = 2.25$, $P = 0.02$) or dense forest (Proportions test, 49% of 61 *P. reidy* and 68% of 88 *P. fera*; $Z = 2.33$, $P = 0.02$) (only 4 *P. reidy* were found in the heath forest, which was not sufficient for a comparison).

The height at which spiders were found on the vegetation (i.e., height > 0 cm) did not differ significantly between adult males (median = 120 cm, $Q_{25} = 40$, $Q_{75} = 150$) and females (median = 45 cm, $Q_{25} = 37$, $Q_{75} = 57$) of *P. reidy* (Mann-Whitney *U*-test, $U = 109$, $P = 0.08$) or between adult males (median = 30 cm, $Q_{25} = 19.5$, $Q_{75} = 49.5$) and females (median = 40 cm, $Q_{25} = 12$, $Q_{75} = 113$) of *P. fera* (Mann-Whitney *U*-test, $U = 40$, $P = 0.74$). There was no difference in the height of juveniles between *P. reidy* (median = 85 cm, $Q_{25} = 49$, $Q_{75} = 150$) and *P. fera* (median = 71 cm, $Q_{25} = 40$, $Q_{75} = 134$) (Mann-Whitney *U*-test, $U = 10,024$, $P = 0.13$); nor

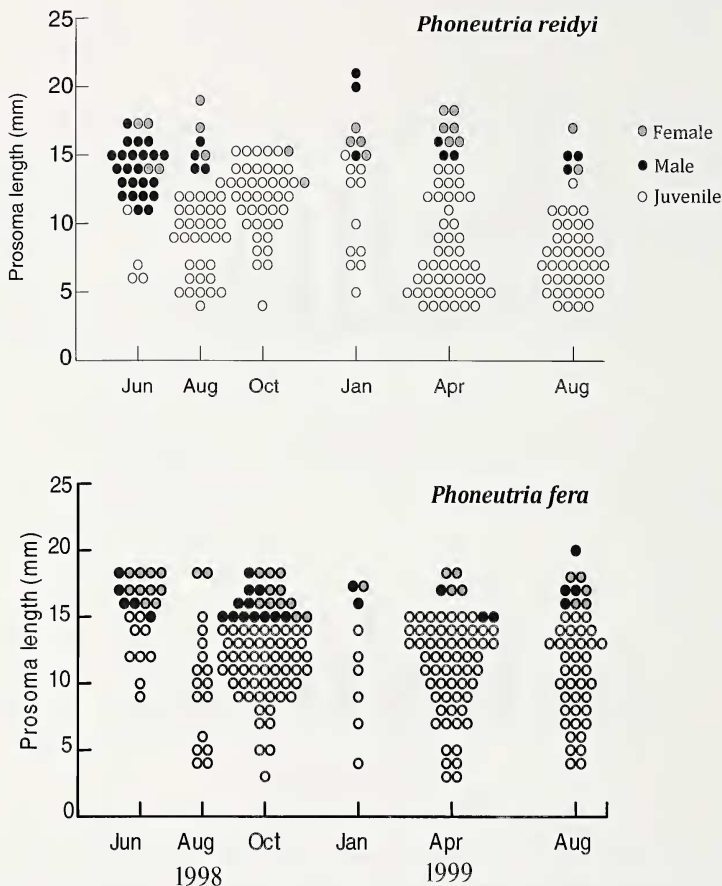


Figure 4.—Distribution of sizes of *P. reidy* and *P. fera* on each of six collection dates during two years.

between females of the two species (Mann-Whitney *U*-test, $U = 42$, $P = 0.56$). However, male *P. reidy* were found in higher places than male *P. fera* (Mann-Whitney *U* test, $U = 169$, $P < 0.001$).

Structure of body size.—There was strong temporal variation in the structure of body size of *P. reidy* (Fig. 4). Comparing data from October 1998 and April 1999, we found a significant difference (Kolmogorov-Smirnov test, $D = 0.57$, $P < 0.001$). This variation indicates a marked seasonal reproduction for *P. reidy*. Another indication of seasonal reproduction was the high proportion of males captured in June 1998 (23♂: 4♀), most of them (93%) being on the ground, which, in this species, could indicate that they were searching for females.

In *P. fera*, the structure of sizes remained relatively constant during the study (Fig. 4). Comparing data from October 1998

and April 1999, we found no significant difference (Kolmogorov-Smirnov test, $D = 0.15$, $P = 0.58$). Apparently, these spiders reproduce throughout the year. Another indication of continuous reproduction in *P. fera* was that the sex ratio did not change much throughout the year, and both males and females were found on the ground in similar proportions (56% and 45% respectively).

DISCUSSION

The abundance of small and acaulescent palms correlated with the abundance of *P. reidy* within habitats; consequently, this factor may explain why this species is abundant in swamp forests, where the palms are abundant and why they are rare in the heath forest, where the palms are almost absent. The association between *Phoneutria* and plants with large leaves, as we have found for *P. reidy*, has been documented in previous

papers (Schiapelli & Gerschman 1972; Bücherl 1980; Lucas 1988). Therefore, more remarkable was the absence of a relationship between the abundance of *P. fera*, collected in similar numbers in the same area, with the abundance of palms.

We propose that the preponderance in use of the vegetation by juveniles of both species is an adaptation to avoid their common ground predators, and that the adults and subadults of *P. reidyi* use the vegetation more frequently, mainly to avoid predation by adults and subadults of *P. fera* on the ground. Barth et al. (1988), working with spiders of the genus *Cupiemi*, found that the palms are probably a safe place to stay because a spider is less visible and more able to sense vibrations of an approaching predator. Small juvenile *P. fera* were almost always on the vegetation; only individuals with a prosoma length greater than 8 mm were found on the ground. This is about the mean size of adults of two important potential predators, *Ctenus amphora* Mello-Leitao 1930 and *Ctenus crulsi* Mello-Leitao 1930, the most abundant medium-sized wandering spiders on the ground (Gasnier et al. 2002). Once *P. fera* spiders grow larger, their dispersal on the ground may be an advantage, because the *Ctenus* spiders will be smaller than them and thus become potential prey. We made no observations of *Ctenus* preying on *Phoneutria*, probably because small individuals were rare on the ground, but similar wandering spiders are among the main prey of *Ctenus*, and we observed that *Ctenus* was among the main prey of medium-sized to large *Phoneutria*. A similar pattern was noted with *P. reidyi*, but they also have *P. fera* as a larger predator on the ground. The mean prosoma length of adult *P. reidyi* (14.4 mm in males and 15.9 mm in females; Gasnier et al. 2002) is inferior to the mean prosoma length of *P. fera* (16.2 mm in males and 16.8 mm in females). Smaller spiders are probably more vulnerable to intraguild predation (Polis et al. 1989) and, consequently, less exposed (Johnson & Sih 2007), which would explain the more intensive use of the vegetation by *P. reidyi*.

Direct evidence from a field experiment is necessary to demonstrate cases of coevolutionary divergence (Connell 1980) like the differentiation in use of the habitat suggested above. Meanwhile, there are additional arguments and evidence to sustain the hypothesis that the interaction between these two species, and possibly among other species of *Phoneutria*, is a relevant factor in their ecology. 1) The absence of a negative association between these sympatric species is not incompatible with this hypothesis because it is possible that coexistence in the present may have been facilitated by differentiation in the use of vegetation under intraguild predation pressure in the past. 2) The seasonality in reproduction of *P. reidyi* is consistent with this hypothesis because males searching for females probably have to disperse more frequently on the ground, and limiting this behavior to a part of the year could be an adaptation to prevent predation by *P. fera*. 3) *P. boliviensis* (F.O. Pickard-Cambridge 1897) is another Amazonian species with the smallest adults of the genus in central Amazonia. We have never seen it in "terra firme" forests, but it is relatively common in periodically inundated forests (T. Gasnier, pers. obs.). 4) Martins & Bertani (2007) showed that sympatry is practically restricted to the distribution limits of four species of *Phoneutria* in southeastern Brazil (only *P. pertyi* [F.O. Pickard-Cambridge 1897] was sympatric with other species). These contiguous

allopatry patterns do not prove, but are consistent with, the importance of intraguild predation in the genus. Field experiments and study of the use of the habitat by sympatric and allopatric populations of *Phoneutria* species are necessary to verify these hypotheses and understand the ecology and evolution of this genus.

Phoneutria may be considered key species in the forests where they occur. Most studies on *Phoneutria* were based on few individuals, probably because adults are not easy to find (Almeida et al. 2000). However, much data on abundance, distribution, and behavior may be acquired when juveniles are included in the study (e.g., Folly-Ramos et al. 1998; present study). Therefore, together with other ctenids, these spiders may be good indicators of disturbance in forest fragments (Jocqué et al. 2005). The ecology of *Phoneutria* is not only important because of its medical importance. Comparative studies may also help to understand the importance of these predators in Neotropical forests.

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